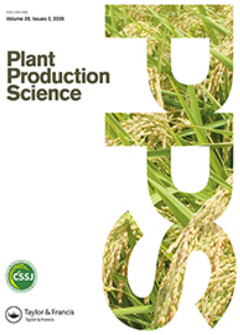

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Seasonal root growth and dry matter partitioning in perennial wheat

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ABSTRACT

Perennial wheats produced grain for up to 4 years in southern Australia, but quantitative data are lacking on dry matter (DM) allocation above- and below-ground over regrowth cycles. This paper examines performance of 4 perennial wheats (147235a [235a], 147280b [280b], OK7211542 [OK72] and 11,955), a perennial grass (148055 [055]), and a replanted-annual bread wheat (Wedgetail) over 3 years in large soil columns. By year 3, total DM increased to 137 g pl^{-1} in perennial wheat and 194 g pl^{-1} in perennial grass, but remained at 55 g pl^{-1} in annual wheat. In the annual wheat, a higher proportion of its root DM was in the 30–60 cm layer with none below 120 cm, while perennial wheats increased their root DM below 60 cm each year, and perennial grass had the most below 120 cm. By the third year, spike DM was 11, 39, 25, 20, 11 and 5 g pl^{-1} for Wedgetail, perennial wheats 11,955, OK72, 235a, 280b, and perennial grass, though Wedgetail was bird damaged. The results demonstrated that perennial wheats could exceed annual wheat in total and especially deep root DM, and with spike DM equalling or exceeding the annual wheat by the third year. Contrary to previous reports, any reduction in performance in later cycles was associated with lower spike DM pl^{-1}, rather than reduced plant stand, following exposure to moderate water deficit in the previous dry season. Annuals and perennials differed in DM allocation; perennial wheat prioritised roots over shoots, until a suitable foundation was established.

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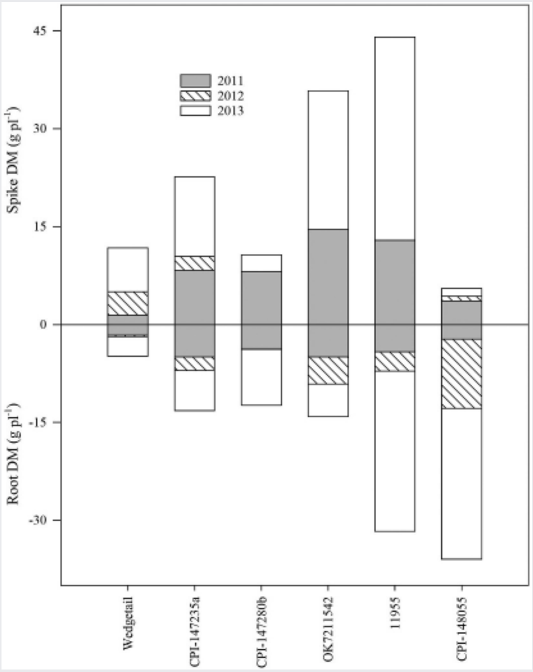

Spike DM (g pl^{-1}) and root DM (g pl^{-1}) for one annual wheat (Wedgetail), four perennial wheats (CPI-147235a, CPI-147280b, OK7211542 and 11,955), and a perennial grass (CPI-148055) grown in large, deep soil columns in 2011 (closed), 2012 (striped) and 2013 (open) at Wagga Wagga NSW, Australia. l.s.d. For spike DM was 8.1 g pl^{-1} and for root DM was 7.3 g pl^{-1} ($p < 0.05$). The results showed that perennial wheat could exceed annual wheat in total and especially deep root DM. Perennial wheat could also produce spike DM equal to or even exceeding the annual wheat by the third year. The results also revealed how DM allocation differed, with perennial wheat prioritising roots over shoots, until a suitable foundation for survival and regeneration was established.

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1. Introduction

The replacement of deep-rooted native perennial vegetation with shallow-rooted annual crops has contributed to hydrological imbalance, nutrient leakage and soil degradation in many dryland farming regions (Glover et al., 2010; Tilman et al., 2011). In southern Australia's wheat – sheep zone, low and variable rainfall, inherently poor soils and reliance on annual crops have allowed water and nutrients to move below the shallow root zone, contributing to rising water tables, soil acidification and salinity (Angus et al., 2001; Turner, 2004). Management options such as reduced tillage, stubble retention, crop rotation and short pasture leys help, but perennial grain crops could further stabilise ground cover and hydrology while producing grain and forage (Bell et al., 2010; Glover et al., 2010). Perennial wheat is especially attractive in this region because wheat is already the dominant cereal in mixed crop – livestock systems.

Preliminary whole-farm bio-economic analysis using the MIDAS model indicated that perennial wheat could be profitable in Australian wheat – sheep systems if its grain yield reached about 65% of annual wheat when priced equally, or about 40% if it also supplied ~0.8 t ha^{-1} of extra forage (Bell et al., 2008). The modelling suggested that annual wheat would remain preferred on the best cropping land, whereas dual-purpose perennial wheat would be favoured on intermediate land classes where early and late grazing could increase lamb survival and carrying capacity (Bell et al., 2008, 2010). These results, together with global assessments of perennial grains, have helped motivate efforts to develop perennial cereals that can contribute both grain and ecosystem services (Chapman et al., 2022; Crews et al., 2018).

Development of perennial wheat has relied on wide hybridisation between annual wheat (*Triticum aestivum* L. [6x], *T. durum* [4x] or *T. carthlicum* [4x]) and closely related perennial grasses such as *Thinopyrum elongatum* [2x], *Th. intermedium* [6x], *Th. ponticum* [8x] and *Agropyron spp*. (>8x), building on early work in the former USSR (Tsitsin & Lyubimova, 1959; Wagoner & Schaeffer, 1990). Breeding programs in North America, China, Australia and elsewhere have subsequently produced numerous experimental lines, particularly from *T. aestivum* × *Th. intermedium* and *T. aestivum* × *Th. ponticum* (Cox et al., 2006; Cui et al., 2018; Hayes et al., 2018; Murphy et al., 2010). Progress has been constrained by complex and unstable genomes, including loss or rearrangement of chromosomes through generations, although there is evidence that retention of more complete chromosome sets from both parents can improve viability and perenniality (Curwen McAdams & Jones, 2017; Larkin et al., 2014).

Field evaluations of perennial wheats have demonstrated both promise and persistent challenges. At Cowra in southern New South Wales, Australia, Hayes et al. (2012) showed that several perennial wheat lines could regrow and produce grain for three consecutive years under rainfed conditions, although many of the 150 entries failed to survive the harsh dry seasons (DS). In a subsequent Cowra study, the highest-yielding lines produced first-year grain yields up to 75% of the annual check Wedgetail, but the best grain producers often failed to regrow, and only four lines persisted and yielded grain across four years (Larkin et al., 2014). In Washington State, USA, the best lines yielded up to 93% of the annual check in the first season (Murphy et al., 2010), whereas in Michigan, perennial lines yielded similarly in years 1 and 2, but only around half the grain yield of annual wheat (Jaikumar et al., 2012). Multi-environment testing of perennial winter cereals confirmed that survival and post – year-1 productivity varied widely, and emphasised the need to select for performance beyond the establishment year (Cattani, 2024; Galassi et al., 2025; Hayes et al., 2018; Morgounov et al., 2025). Several reports noted that plant stand declined in perennial wheat in each DS, while plant stand was maintained in the perennial grass (Hayes et al., 2012; Larkin et al., 2014; Newell & Hayes, 2017). Consequently, these authors associated the decline in grain yield in perennial wheat with decline in plant stand, rather than yield per plant.

A central unresolved issue is whether perennial growth habit necessarily imposes a trade-off with grain yield. Perennial cereals must invest carbon and nutrients into regenerative structures such as crowns, roots, rhizomes and axillary buds to support regrowth, potentially diverting resources from reproductive sinks (Cassman & Connor, 2022; Loomis, 2022). Conversely, once established, their deeper and more persistent root systems may allow access to additional water and nutrients below the rooting zone of annual crops, partly offsetting any allocation penalty and enabling both regrowth and acceptable grain production (Ewel et al., 2018; Glover et al., 2010; Huang et al., 2025). Despite increasing evidence for enhanced root biomass and ecosystem services in perennial grain systems, quantitative data on dry-matter (DM) production, above- and below-ground partitioning, and water extraction over successive regrowth cycles are still scarce for perennial wheat and other perennial grain crops.

This study is the first in a series examining resource capture and DM allocation in perennial wheat and related cereals. Here we focus on quantifying seasonal DM production and partitioning in four perennial wheat lines, a perennial grass and an annual wheat check (replanted each year), grown in large, deep soil columns under well-watered conditions over three years. Additional soil columns allowed regular destructive sampling to characterise root growth, as well as a subsidiary experiment that imposed moderate DS water deficit to test carry-over effects on subsequent wet season (WS) performance. The results are interpreted alongside field performance of the same genotypes at Cowra and other perennial versus annual cereal comparisons, with particular emphasis on trade-offs and opportunities associated with perennial growth habit.

2. Materials and methods

2.1. Experiment location and soil column preparation

This study was conducted outdoors in large soil columns in an open-topped, side-netted enclosure in the Horticulture Precinct at Charles Sturt University, Wagga Wagga NSW, Australia (35.05°S, 147.35°E, 219 m). Soil columns were established using 1.50 m long, white PVC tubes with an internal diameter of 0.10 m. Each tube was filled with homogenised granitic loamy-sand to a bulk density of 1.7 Mg m^{-3} The soil had pH 7.2 (1:5 soil/water), 1.82% total organic C, 0.305% total Kjeldahl N, 20.0 mg kg^{-1} available P (Colwell), 0.345 cmol kg^{-1} exchangeable K, 1.90 cmol kg^{-1} exchangeable Ca, 0.255 cmol kg^{-1} exchangeable Mg, 0.165 cmol kg^{-1} exchangeable Na, effective cation exchange capacity 2.50 cmol kg^{-1} and electrical conductivity 53.5 mS cm^{-1} (1:5 soil/water). Each soil column had a total volume of 1.18×10^{-2} m^3, a surface area of 7.86×10^{-3} m^2, and a soil mass of 26.0 kg at field capacity. A hole was drilled in the basal sealed cap of each column to allow drainage of excess water onto the concrete floor. Roots could not access soil from below the columns.

2.2. Experimental design and selection of genotypes

The experimental design was a split-plot with six genotypes replicated three times as the basis of each sampling unit, giving 20 sampling units available for destructive measurements over the three-year period. The six genotypes comprised one annual bread wheat, four perennial wheat lines and one perennial grass.

The annual wheat control was *Triticum aestivum* L. cv. 'Wedgetail', a dual-purpose winter-type longer-duration bread wheat developed for the wheat-sheep farming system of southern Australia. Four perennial wheat lines were selected which differed in the source of the perennial grass parent: CPI-147235a (235a; *Th. ponticum*); CPI-147280b (280b; *Th. intermedium*); OK7211542 (OK72; *Th. ponticum*); 11,955 (11,955; *Th. ponticum*). While these perennial wheats each had 56 chromosomes, the contribution from each parent varied: not known for 280b (*T. carthlicum* × *Th. intermedium* × *T aestivum*); 42 *T. aestivum* and 14 *Th. ponticum* for 235a and OK72; but only 40 *T. aestivum* and 16 *Th. ponticum* for 11955 (Cox et al., 2002; Curwen McAdams et al., 2016; Morgan et al., 2023). Each of these lines had previously demonstrated the ability to regrow and produce grain over three to four years under field conditions at Cowra, NSW (Hayes et al., 2012; Larkin et al., 2014).

Intermediate wheatgrass CPI-148055 (055; *Th. intermedium*) was chosen as the perennial grass control, because of its strong regrowth and its common use as a parent to confer perennial growth habit. Thus, Wedgetail and CPI-148055 also represented the annual and perennial 'parent' types used to develop the perennial wheats.

2.3. Cultural management

Seeds, treated with the fungicide Baytan T® (active ingredients Triadimenol 150 g L^{-1} and Triflumenol 150 g L^{-1} at 100 ml per 100 kg), were sown on 7 May 2011. After emergence, stands were thinned to one plant per column. In subsequent years, the annual wheat was resown into the columns allocated to the annual wheat treatment in all remaining sampling units, on 5 May 2012 and 8 May 2013, respectively. This allowed WS comparisons between annual and perennial entries. As the annual wheat did not regrow, however, it was absent from DS comparisons. At the end of each growing season, in about December (the end of the WS) and May (the end of the DS), the stubble was cut back to 0.08–0.10 m, removed and recorded. This ensured regrowth of perennial genotypes from a consistent base in the following season, and discouraged tillering from higher nodes.

Irrigation was supplied via a dripper to each soil column. For the well-watered treatment, soil columns were irrigated to field capacity at fortnightly intervals throughout the experiment, using a load cell to determine the amount of water required to return the columns to target weight. For the DS water-deficit treatment, selected columns were irrigated at monthly intervals during the DS only (December to April), from grain harvest at the end of one WS, until removal of DS biomass at the commencement of the next WS. Any rainfall event that effectively replaced a scheduled irrigation was counted as a watering event, and subsequent watering dates were recalculated. Fortnightly irrigations resumed for all treatments during each WS.

At monthly intervals, 30 mL of solution containing an all-purpose soluble fertiliser (5 g Yates Thrive [25 N: 5 P: 8.8 K] in 1.8 L water) was applied to each column at the time of irrigation. When required, the insecticide Confidor (0.125 g L^{-1} Imidacloprid) was sprayed to control leaf-sucking insects, and fungicide Bumper (418 g L^{-1} Propiconazole) was applied against leaf rusts.

2.4. Measurements

Total DM production and allocation between above- and below-ground components were quantified at six harvests, timed according to developmental progress of each genotype in each growth cycle. In the first year, two harvests were taken: Harvest 1 at flowering in October – November 2011 (2011a), and Harvest 2 at maturity in November – December 2011 (2011b), both during the first WS. In the second year, Harvest 3 was taken at the end of the DS in April 2012 (2012a), and Harvest 4 at maturity at the end of the WS in November – December 2012 (2012b). In the third year, Harvest 5 was taken at the end of the DS in April 2013 (2013a), and Harvest 6 at maturity at the end of the WS in November – December 2013 (2013b). For each genotype, the dates of flowering and maturity (growth stages 65 and 89, respectively; Zadoks et al., 1974) were recorded. Plant height, and tiller and spike number pl^{-1}, were also recorded.

At each harvest, shoots were cut at the soil surface and separated into crowns, leaves and stems, and spikes, to quantify above-ground biomass allocation. At maturity, grains were separated from spikes and cleaned by hand using a customized tabletop thresher. At the same time, PVC tubes were cut longitudinally to expose the soil columns, which were then cut into 0.10 m sections. After soaking in Calgon® solution, each depth increment was washed to remove soil using a mechanised root washer (Benjamin & Nielsen, 2004), and roots were collected on a 1 mm mesh sieve. All plant components were dried at 70°C for 48 h and DM recorded, with grain DM adjusted to 14% moisture. Because very few roots were present in the 2012 DS, root data were not collected for the 2013 DS, to preserve the remaining cores for subsequent measurements. Random subsamples of 100 grains were counted to determine mean single-grain mass.

The annual wheat Wedgetail was severely damaged by birds. This occurred despite efforts to place netting over individual replicates, and to bag individual ears. More robust netting systems were installed in the third year, however grain DM of Wedgetail was still underestimated, while other entries did not attract bird-feeding activity.

2.5. Statistical analysis

Statistical analyses were conducted using GenStat 16th edition (GenStat® for Windows 10.0, VSN Int. Ltd, UK, 2013). For each trait, data were analyzed as a split-plot with repeated harvests. Harvest was tested against main-plot error, whereas genotype and the genotype × harvest interaction were tested against residual error. Treatment means were compared using least significance difference (l.s.d.; $p < 0.05$ or $p < 0.01$) with appropriate error degrees of freedom (Steel & Torrie, 1960). Linear regressions were used to further explore relationships among traits.

3. Results

3.1. Cultural conditions

Maximum and minimum temperature, relative humidity, rainfall, pan evaporation and potential evapotranspiration data for the study period are presented in Figure 1. Weather parameters were generally similar to the long-term average, with mean monthly maximum and minimum temperatures varying from a maximum of 44°C in January to a minimum of −5°C in July. The hottest summer occurred in the 2013 DS. Although the average annual rainfall at the experimental site during this three-year study was 487 mm, which was slightly lower than the long-term mean (572 mm), irrigation was applied fortnightly throughout (WW, well-watered), or monthly in the DS only (WD, water-deficit).

3.2. Overall data summary

All sources of variation were statistically significant for all traits ($p < 0.05$; $p < 0.01$), except for the harvest ×genotype interaction for spike number pl^{-1}, grain number $spike^{-1}$, stem and leaf DM, and shoot DM (Table 1). In general, the perennial wheat lines 235a and 11,955 and the perennial grass 055 had greater shoot DM, but the perennial wheat OK72 and the annual wheat Wedgetail had higher HI, even though the annual wheat Wedgetail was severely bird damaged. Grain size was large in perennial wheat 11,955 (34.4 mg) and annual wheat Wedgetail (29.0 mg), intermediate in the other perennial wheats (15.7–22.5 mg), and low in the perennial grass 055 (4.4 mg), which also had fewer grains pl^{-1}. While the annual wheat had the lowest root dry matter, the perennial grass 055 had the highest tiller number pl^{-1} and

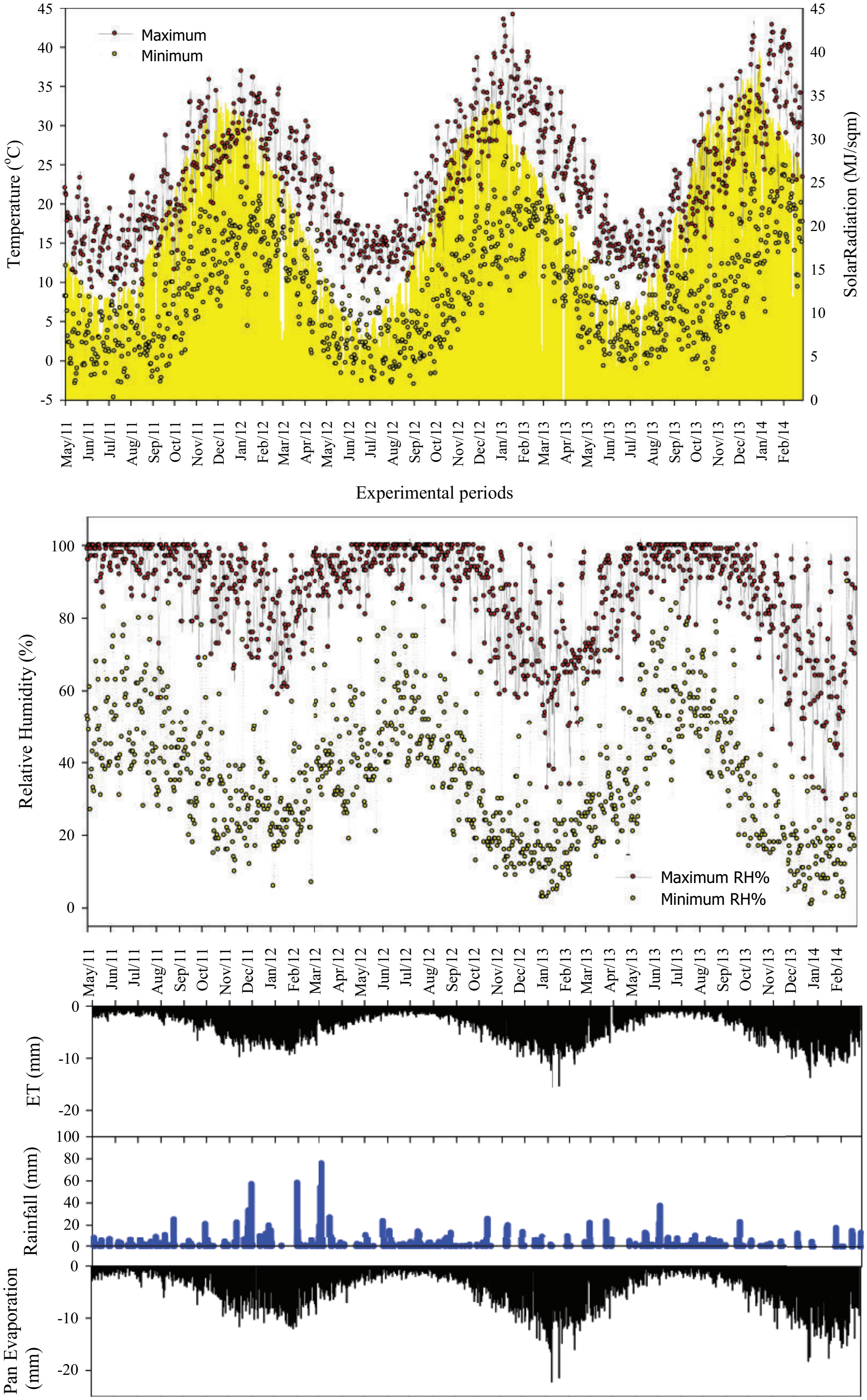

Figure 1. a) Mean monthly maximum and minimum temperature (°C) and solar radiation (MJ m^{-2}), b) maximum and minimum relative humidity (%), c) rainfall (mm) and evapotranspiration (et; mm), and d) pan evaporation (mm), from May 2011 to February 2014 at Wagga Wagga NSW, Australia.

Table 1. Main effects of Harvest (2011, 2012 and 2013 wet seasons [WS]), genotype (Wedgetail, 147235a, 147280b, OK7211542, 11,955, 148,055) and Harvest x genotype (H x G) for 1 annual wheat, 4 perennial wheats and 1 perennial grass grown in large soil columns in the enclosure in the horticultural precinct at Charles Sturt University in Wagga Wagga NSW Australia in 2011, 2012 and 2013.

Source	Plant height (cm)	Tiller number (pl^{-1})	Spike number (pl^{-1})	Grain number (pl^{-1})	Grain number (spike^{-1})	Grain size (mg)	Root depth (cm)	Root DM (g pl^{-1})	Crown DM (g pl^{-1})	Stem & Leaf DM (g pl^{-1})	Spike DM (g pl^{-1})	Shoot DM (g pl^{-1})	Harvest Index (%)	Grain DM (g pl^{-1})
Harvest (H)														
2011 WS	84.9	27.5	13.1	109.6	9.3	14.6	87	3.8	3.5	28.7	8.4	40.7	5.3	2.02
2012 WS	97.8	27.4	15.1	193.2	15.2	21.9	141	11.3	4.9	27.8	7.3	42.8	20.8	4.28
2013 WS	98.3	54.4	28.8	397.1	19.7	25.1	137	18.3	16.2	63.9	21.5	93.9	20.5	11.70
l.s.d.	*8.6***	*6.5***	*7.1***	*35.8***	*8.4* ^{ns}	*3.3***	*11.3***	*3.0***	*3.5***	*19.0***	*3.3***	*22.5***	*10.6***	*1.34***
Genotype (G)														
Wedgetail	79.2	10.4	7.4	148.6	20.7	29.0	103	2.8	1.2	13.7	6.1	21.1	25.2	4.63
147235a	104.1	32.8	18.8	296.3	15.4	15.7	127	9.5	5.7	50.1	14.4	70.1	10.7	5.49
147280b	79.2	24.1	13.8	162.9	19.5	17.1	126	8.8	4.4	27.9	7.2	38.0	17.8	2.74
OK7211542	103.1	37.7	21.7	406.3	16.6	22.5	133	10.2	7.1	32.6	19.5	47.4	27.1	10.13
11,955	103.5	45.1	25.9	349.2	14.2	34.4	129	15.2	9.6	58.7	22.7	94.2	12.0	12.83
148,055	93.0	68.3	26.1	36.6	2.1	4.4	111	20.3	21.3	57.7	4.5	84.0	0.4	0.17
l.s.d.	*12.1***	*9.1***	*10.0***	*50.6***	*11.8**	*4.7***	*16.2***	*4.2**	*5.0***	*26.9***	*4.7***	*31.9***	*7.5***	*1.90***
H x G														
l.s.d.	*21.0**	*15.8***	*17.3*^{ns}	*87.7***	*20.5*^{ns}	*8.1***	*33*^{ns}	*7.3***	*8.6***	*46.6*^{ns}	*8.1***	*55.2*^{ns}	*18.4***	*3.29***
Overall Mean	**93.7**	**36.4**	**19.0**	**233.3**	**14.7**	**20.6**	**122**	**11.1**	**8.2**	**40.1**	**12.4**	**59.1**	**15.5**	**6.00**

the greatest root DM. In the perennials, maximum root depth was greater and increased in subsequent years.

3.3. *Days to flowering, plant height, tillers per plant and spikes per plant*

All genotypes established well after planting in May 2011. Flowering in the first wet season (WS) occurred at about 175 days after sowing in the perennial wheat derivatives, with the annual wheat about 15 days earlier, and the perennial grass about 10 days later (Figure 2(a-c)). In the perennial wheats, flowering occurred on average at 180, 180 and 150 days over the three years, several days earlier in Wedgetail annual wheat, and later in perennial grass 055, especially in year 3. Except for the perennial grass 055, which flowered at around 200 days in each season, time to flowering decreased in the third year, by about 20 days in 235a and about 30 days in the other perennial wheats. For plant height (Figure 2(d-f)), perennial wheats OK72, 235a and 11,955 were about 20 cm taller than the other entries in the first wet season. Differences in plant height increased in the second WS, with perennial grass 055 joining the tall group which averaged 110 cm, while 280b was 85 cm and Wedgetail was 65 cm. Differences in plant height were not statistically significant in year 3, ranging from 85 to 110 cm.

On average, there were about 30 tillers pl^{-1} in the first WS (Figure 3(a-c)), with fewer in Wedgetail, and more in OK72. Wedgetail consistently had the fewest tillers, averaging 12 pl^{-1} over the three seasons. There tended to be an increase in the number of tillers pl^{-1} in the perennial wheats with time, especially in 11,955 in year 3. Likewise, in the perennial grass 055, there was a large increase to 135 tillers pl^{-1} in the third year. The number of spikes pl^{-1} (Figure 3(d-f)) was about half the number of tillers pl^{-1} in the first year, with fewer spikes in Wedgetail, and more in OK72 and 11,955. In Wedgetail, the number of spikes pl^{-1} remained consistently low in years 2 and 3, while the number of spikes pl^{-1} generally increased in the perennials with time, especially in 11,955 and 055, each having about 45 spikes pl^{-1} in the third year.

3.4. *Total dry matter production and partitioning above- and below-ground*

During the 2011 WS, total dry matter increased from about 30.1 g pl^{-1} at flowering (Figure 4(a)) to about 42.4 g pl^{-1} at maturity (Figure 4(b)), with the perennial wheats exceeding the perennial grass 055 and the annual wheat Wedgetail. In the annual wheat Wedgetail, however, grain DM at maturity was penalised by severe bird damage in all three years, despite efforts to protect grain by netting and bagging individual spikes. During the 2012 DS, regrowth was absent in annual wheat and limited to about 19.9 g pl^{-1} in the perennial genotypes, despite fortnightly irrigations (Figure 4(c)). In the 2012 WS, shoot DM was generally similar to the 2011 WS, but was reduced in 280b and increased in 055, while root growth increased in the perennials, especially in the perennial grass 055 (Figure 4(d)). By the third year, these responses were

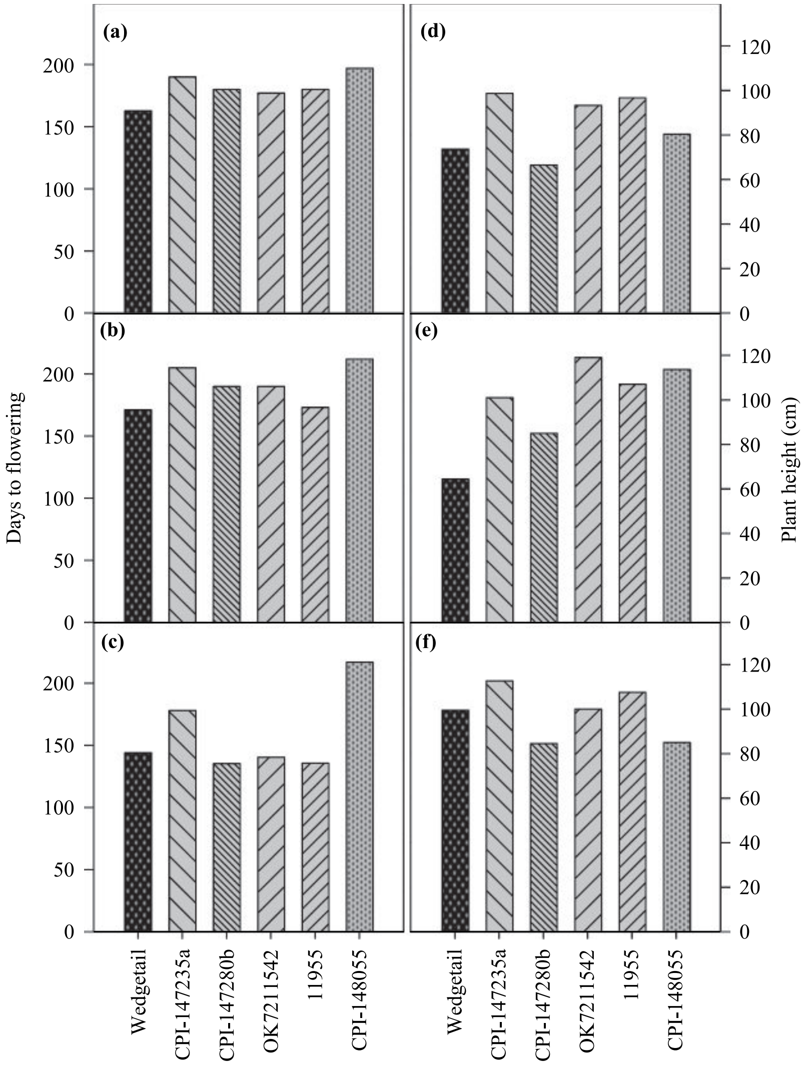

Figure 2. Time from sowing/stubble cut to flowering (days; a, b, c), and plant height (cm; d, e, f); for one annual wheat, four perennial wheat lines and one perennial grass, in the 2011 (a, d), 2012 (b, e) and 2013 (c, f) wet seasons. l.s.d. were 3 days for time to flowering and 21 cm for plant height ($p < 0.05$).

exacerbated, with minimal regrowth of about 3.2 g pl^{-1} observed in the perennials in the 2013 dry season, again despite fortnightly irrigation (Figure 4(e)). In the 2013 WS, dry matter production was greatly enhanced among the well-established perennials, with 235a, 11,955 and 055 averaging about 170 g pl^{-1} (Figure 4(f)). Root DM was always least in annual wheat Wedgetail (4.8 g pl^{-1}), but increased significantly during the third WS in the perennials, and especially in perennial wheat 11,955 and perennial grass 055 (33.8 g pl^{-1}). In the perennial wheats, much of the additional shoot DM was allocated to stem and leaf, though in the third WS, spike and crown DM also increased. Conversely, the perennial grass 055 accumulated less DM in the first wet season, but by the third WS, had equivalent DM to the leading perennial wheats 235a and 11,955, but allocated less to spike, and more to crown (50 g pl^{-1}) and root (35 g pl^{-1}).

3.5. Allocation of root dry matter to different soil depth increments

Over all genotypes and seasons, about 66% of root DM was in the 0–30 cm soil layer, with each subsequent layer having about a third of the layer above (Table 2). There was a greater proportion of roots in shallow layers in year 1, but the proportion of roots in deeper layers increased in year 2. The annual wheat Wedgetail had a higher proportion of roots in the 30–60 cm layer, but a lower proportion in deeper layers below 90 cm, with none below 120 cm. The perennial wheats generally had more roots in the surface layer in year 1, then more in deeper layers in year 2, but in year 3, there was a new flush of shallow roots after the second DS, and thus, a proportionate decrease at depth in year 3. Nevertheless, due to the greater total DM in year 3 in the perennials, this still translated to their greater root

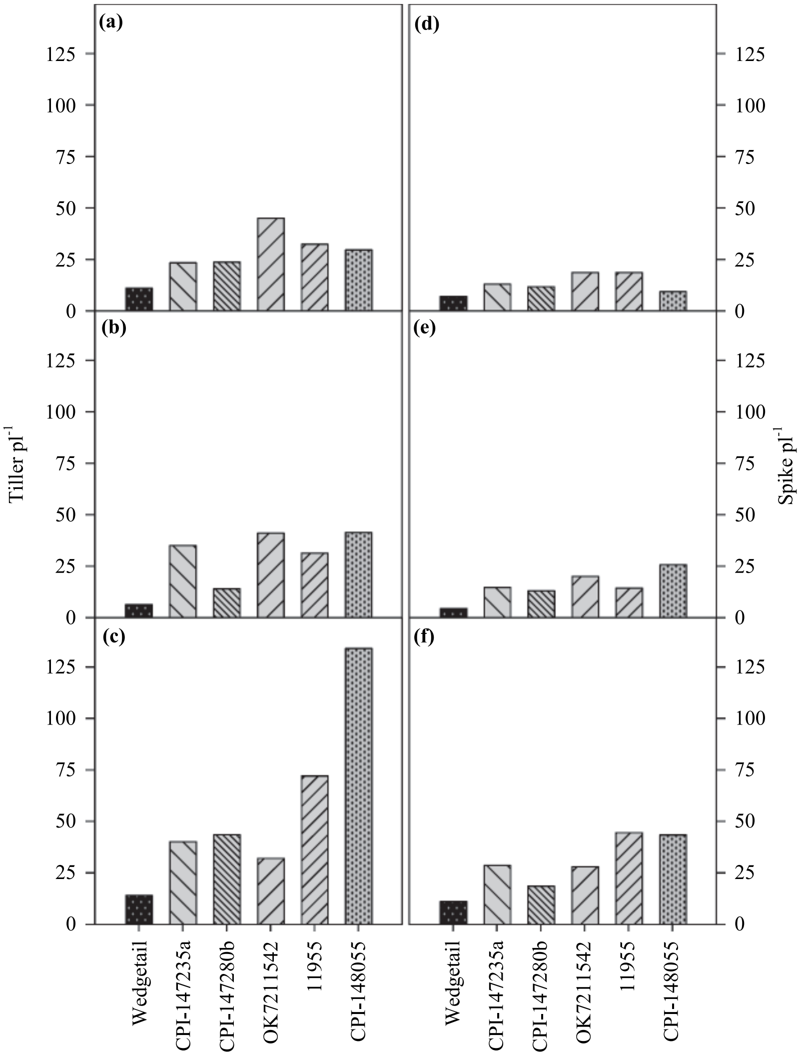

Figure 3. Tillers pl^{-1} (a, b, c) and spikes pl^{-1} (d, e, f) for one annual wheat, four perennial wheat lines and one perennial grass in the 2011 (a, d), 2012 (b, e) and 2013 (c, f) wet seasons. l.s.d. were 16 for tillers pl^{-1} and 7 for spikes pl^{-1} ($p < 0.05$).

DM in year 3, with more in deeper layers in 11,955 and 055. Conversely, the perennial grass 055 had a higher proportion of roots in the surface layer (75.7%), fewer from 30–90 cm (8.2%), but more in the deepest layers, especially 120–150 cm (4.0%).

Wedgetail annual wheat never had roots below 120 cm depth, and its total root DM was consistently low (Figure 5). In contrast, roots of the perennial wheats were present in deeper soil layers, and over the three years of the experiment, their root DM increased on average from 0.0 to 6.75, 0.0 to 1.75, and 0.0 to 1.05 g pl^{-1} in soil layers 0 to 60, 60 to 120, and 120 to 150 cm, respectively. Interestingly, perennial wheat 11,955 had the highest root DM at intermediate soil depths in year 3. Overall, the perennial grass 055 had the highest root DM, even during DS regrowth (Figure 5(c)), and especially below 100 cm soil depth (Figure 5(d,f)).

3.6. Spike dry matter and grain dry matter per plant

Amongst the perennial wheat lines, spike DM (Figure 6(a-c)) ranged from 5–10 g pl^{-1} in the 2011WS and 2012WS, but by the 2013WS, spike DM ranged from 11 g pl^{-1} in 280b, to 20 g pl^{-1} in 235a, 25 g pl^{-1} in OK72, and 39 g pl^{-1} in 11,955. In contrast, spike DM increased from 1 to 5 to 11 g pl^{-1} in the annual wheat Wedgetail, as bird damage was progressively reduced over seasons, but could not be eliminated, while in the perennial grass 055, spike DM was consistent at about 5 g pl^{-1} (Figure 6(a-c)).

Amongst the perennial wheat lines, grain DM (Figure 6(d-f)) averaged about 2 g pl^{-1} in year 1, except for 11,955, which yielded 7 g pl^{-1}. Grain DM began to diverge in year 2, and by year 3, 11,955

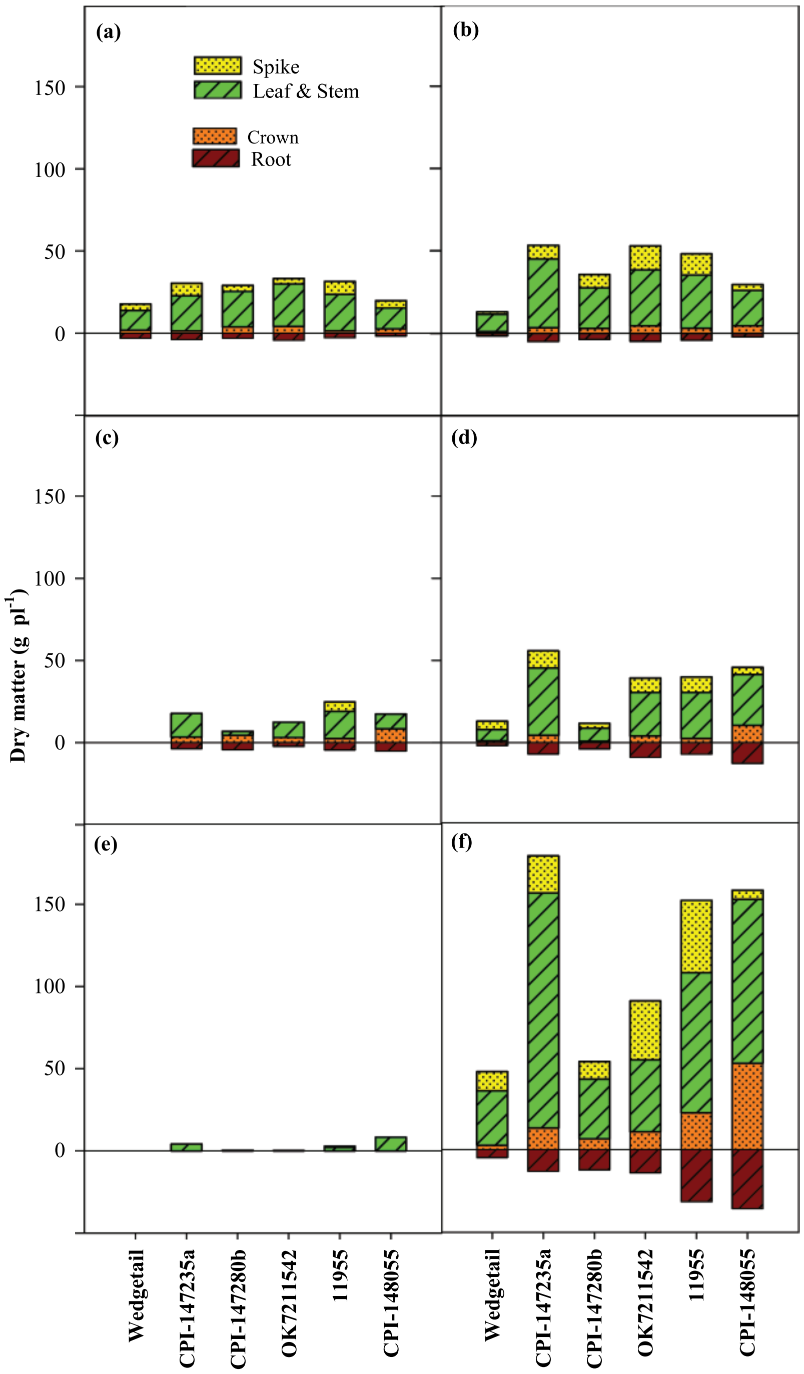

Figure 4. Total above-ground DM (including crown, leaf and stem, and spike) and total root DM for one annual wheat, four perennial wheat lines and one perennial grass: a) at flowering in the 2011 WS; b) at maturity in the 2011 WS; c) at the end of the 2012 DS; d) at maturity in the 2012 WS; e) at the end of the 2013 DS; and f) at maturity in the 2013 WS. l.s.d. were 22.5 g pl^{-1} for total above-ground DM and 7.3 g pl^{-1} for total root DM ($p < 0.05$; see Table 1).

yielded about 26 g pl^{-1}, OK72 about 22 g pl^{-1}, with 235a yielding about 10 g pl^{-1}, and 280b only 3 g pl^{-1}. Grain DM from the perennial grass 055 was always negligible. With bird damage, grain DM in Wedgetail only ranged from 1 to 7 g pl^{-1} over the three wet seasons (Figure 6(a-c)). Harvest index, grain number per spike and individual grain DM were all highly variable (not shown).

3.7. Dry season regrowth under well-watered and water-deficit conditions

Regrowth in the DS was about 13.7% of WS regrowth in year 2, but only about 1.4% of WS regrowth in year 3 (Figure 7). During the 2012 DS, shoot DM was similar under water deficit and well-watered (Figure 7(a)), but in the following 2012 WS, shoot DM was 18% lower following

Table 2. Maximum root depth (MRD – cm), and percentage allocation of root dry matter (RDM - %) to each soil depth increment (0–30, 30–60, 60–90, 90–120, 120–150), for 1 annual wheat (Wedgetail), 4 perennial wheats (147235a, 147280b, OK7211542, 11,955) and 1 perennial grass (148055) grown in large soil columns in the enclosure in the horticultural precinct at Charles Sturt University in Wagga Wagga NSW Australia in 2011, 2012 and 2013.

Source	Wedgetail	*Annual*	147235A	147280B	OK7211542	11,955	*Perennial*	148,055	*Grass*	Mean	MEAN
MRD (cm)											
WS1	70		95	100	100	100		70		**89**	
WS2	90		150	140	150	150		150		**139**	
WS3	120		150	150	150	150		150		**145**	
MRD		***93***					***132***		***123***		**124**
RDM$_{0-30}$ (%)											
WS1	78.2		61.0	80.2	66.3	66.4		89.6		**73.6**	
WS2	56.0		50.1	63.6	48.0	49.4		57.5		**54.1**	
WS3	62.0		64.1	77.7	67.2	66.6		80.0		**69.6**	
Mean		***65.4***					***63.4***		***75.7***		**65.8**
RDM$_{30-60}$ (%)											
WS1	20.7		26.7	16.3	26.6	28.0		8.3		**21.1**	
WS2	30.7		20.6	24.2	20.6	24.7		13.9		**22.4**	
WS3	24.1		22.3	14.9	21.2	18.4		9.9		**18.5**	
Mean		***25.2***					***22.0***		***10.7***		**20.7**
RDM$_{60-90}$ (%)											
WS1	1.1		12.1	3.4	6.6	4.8		2.0		**5.0**	
WS2	13.4		14.4	6.1	16.8	17.0		10.7		**13.1**	
WS3	10.9		9.1	5.1	9.0	10.7		4.5		**8.2**	
Mean		***8.5***					***9.6***		***5.7***		**8.8**
RDM$_{90-120}$ (%)											
WS1	0.0		0.0	0.1	0.6	0.9		0.0		**0.3**	
WS2	0.0		9.6	4.7	9.3	6.5		8.4		**6.4**	
WS3	3.1		4.0	1.6	1.7	3.2		2.8		**2.7**	
Mean		***1.0***					***3.5***		***3.7***		**3.1**
RDM$_{120-150}$ (%)											
WS1	0.0		0.0	0.0	0.0	0.0		0.0		**0.0**	
WS2	0.0		5.4	1.4	5.3	2.4		9.5		**4.0**	
WS3	0.0		1.2	0.7	0.9	1.1		2.5		**1.1**	
Mean		***0.0***					***1.5***		***4.0***		**1.7**

water deficit (Figure 7(b)). In the 2013 DS, shoot DM was lower than in the 2012 DS, especially under water deficit, while the perennial grass 055 had the highest shoot DM in well-watered (Figure 7(c)). In the 2013 WS, shoot DM doubled on average compared with the 2012 WS, but shoot DM was 54.5% lower following DS water deficit compared with well-watered (Figure 7(d)). Genotypes varied in the reduction in WS shoot DM following DS water deficit in 2013, from 42.8% in perennial grass 055 to 72.2% in perennial wheat 235a (Figure 7(d)).

4. Discussion

4.1. Environmental conditions and seasonal regrowth

Regrowth was successful over three consecutive WS in perennial wheats and perennial grass, as indicated by the numbers of tillers pl^{-1} (Figure 3(a-c)) and their total DM (Figure 4(b,d,f)). Despite the perennial wheats evaluated here being selected from cool-temperate-adapted winter wheats in the USA, they were able to survive and regrow for three years in large rewatered soil columns in an open-topped enclosure in this study (Figure 4), and for up to four years at Cowra under Mediterranean field conditions (Hayes et al., 2012; Larkin et al., 2014). The soil column (0.10 m diameter and 1.50 m depth) was intended to be indicative of the root zone available to an individual wheat plant in the field in Australia, where row spacings of 0.20–0.30 m and inter-plant spacings in the row of 0.075–0.010 m are common. Seminal roots grow downwards, and nodal roots soon turn downwards, so we consider it unlikely that root growth could have been significantly impeded in these large, deep, 26.0 kg soil columns, though this should be tested.

While the winters were cool and wet in southern Australia, summers were hot and dry, with high evaporative demand (Figure 1). Consequently, regrowth was limited in all perennial entries in the 2012 and 2013 DS, with few tillers pl^{-1} (data not shown) and reduced biomass accumulation (Figure 4(c,e)), especially in the 2013 DS, when temperatures were substantially higher (from November 2012 to April 2013; Figure 1). Seasonal reduction in regrowth has also been observed in perennial rice in southern China, with only the warmer DS cycle harvested in the cooler and higher altitudes, both DS and WS cycles harvested at lower altitudes with more favourable temperatures, and only the WS cycles harvested in more tropical conditions with a long, hot DS (Huang et al., 2018; Zhang et al., 2017, 2019). Indeed, under the harsher DS

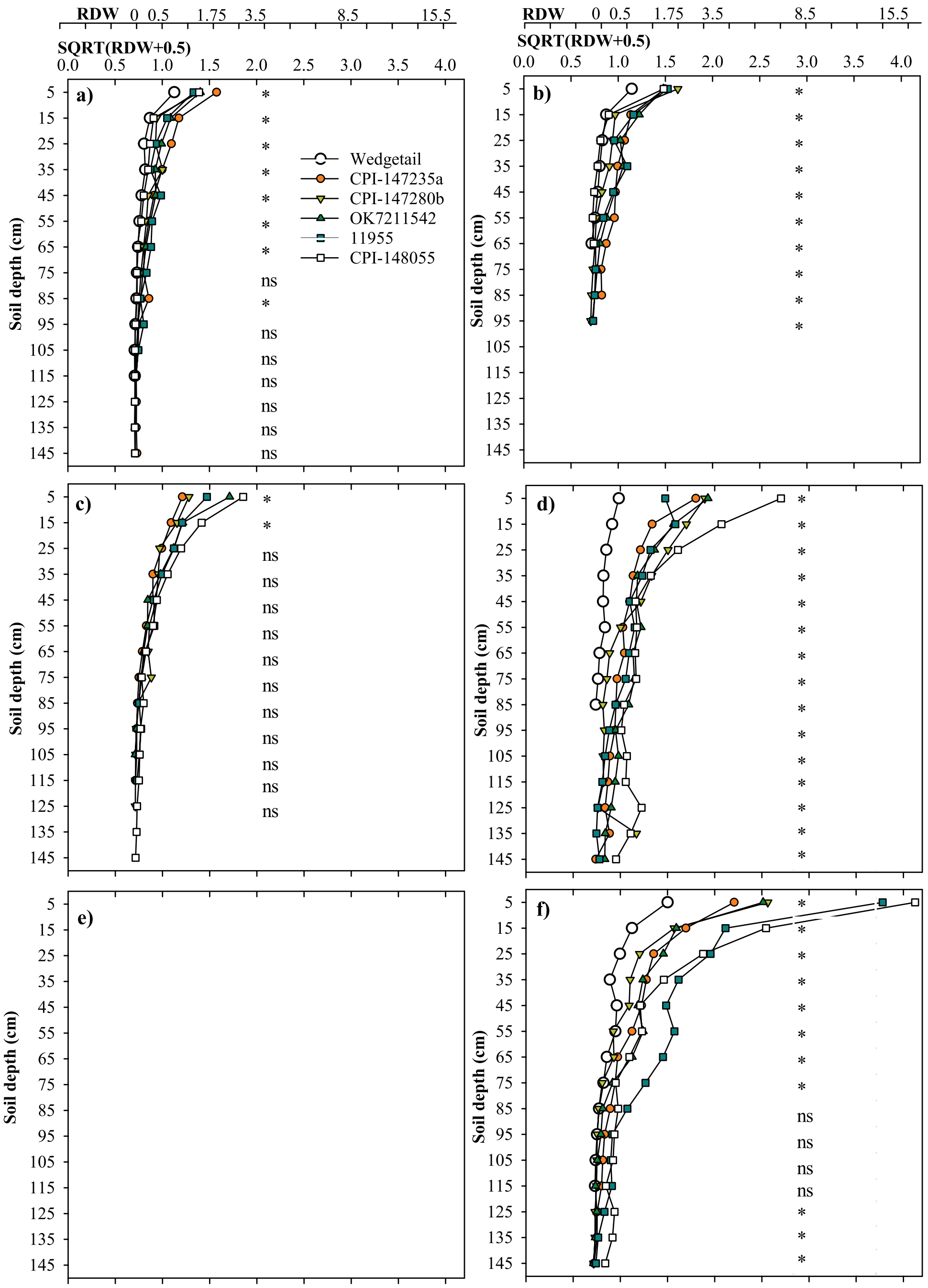

Figure 5. Root DM (RDM), presented as sqrt (RDM +0.50), for 0.10 m depth increments from 0.00–1.50 m soil depth: a) at flowering in the 2011 WS; b) at maturity in the 2011 WS; c) at the end of the 2012 DS; d) at maturity in the 2012 WS; e) at the end of the 2013 DS (data not collected); and f) at maturity in the 2013 WS. In the upper X-axis scale, RDM is shown as (g pl^{-1}), matching the lower X-axis scale for the same data, which are plotted as sqrt (RDW +0.5) below, for treatment separation. For each depth increment, * is statistically significant and n.s. is not ($p < 0.05$).

conditions in southern Lao PDR, perennial rice was only able to contribute grain in two successive WS (the sown crop and one regrowth cycle; Samson et al., 2018). Hence, in both perennial wheat and perennial rice, high temperature constrained DS regrowth, even though adequate irrigation water had been provided. These outcomes suggest that regrowth in perennial grain crops may be limited under conditions of high temperature and high evaporative demand in the DS, even when water is supplied, perhaps due to aerial tissue dehydration, but this needs to be examined further. Nevertheless, reliance on tissue dehydration alone would not be expected to be a reliable strategy for restricting regrowth and resource use in the DS.

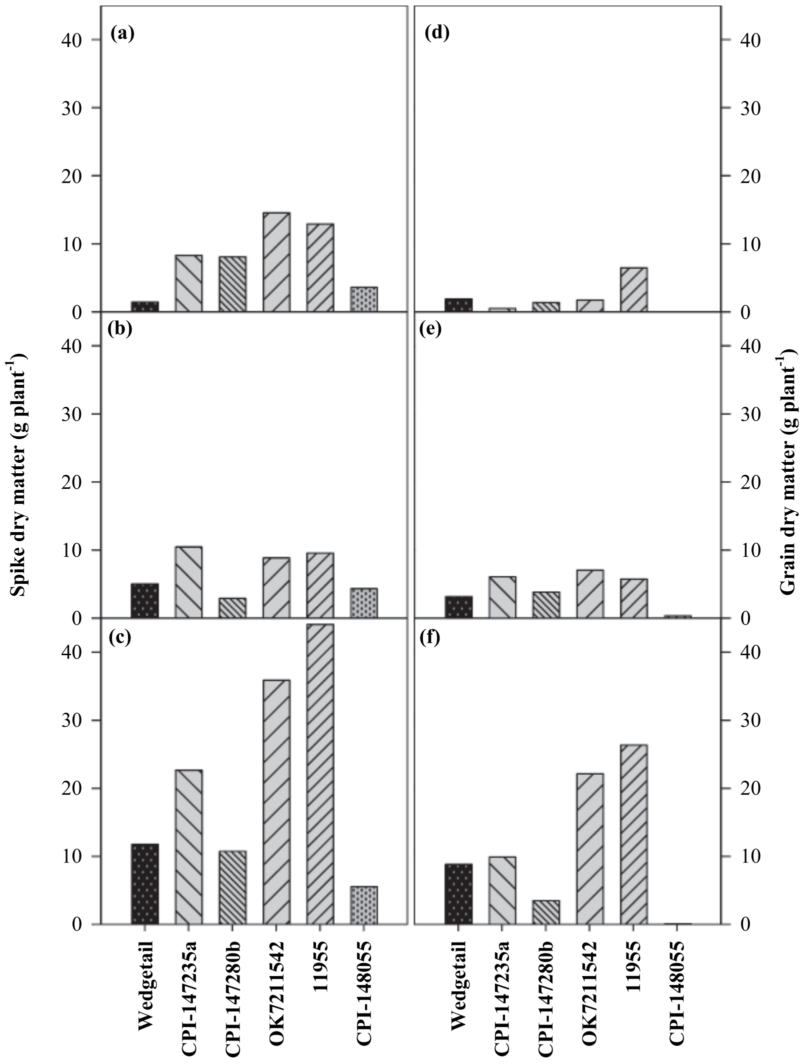

Figure 6. Spike DM (g pl^{-1}; a, b, c) and grain DM (g pl^{-1}; d, e, f) for one annual wheat, four perennial wheat lines and one perennial grass in the 2011 (a, d), 2012 (b, e) and 2013 (c, f) wet seasons. Unfortunately, bird damage reduced spike DM and especially grain DM in annual wheat Wedgetail. l.s.d. were 8.1 g pl^{-1} for spike DM and 3.3 g pl^{-1} for grain DM ($p < 0.05$).

4.2. Production of dry matter

The accumulation of DM was much greater in the perennials, especially in 235a 11,955 and the perennial grass 055, and especially in the third year, while there was little change over years in the replanted annual (Figure 4), which was consistent with earlier reports (Hayes et al., 2012; Larkin et al., 2014). The additional biomass from perennial wheat easily exceeded the critical value of 0.8 t ha^{-1} identified by Bell et al. (2008), which was consistent with the results from defoliation experiments at Cowra (Newell & Hayes, 2017). Thus, perennial wheat should be able to contribute additional forage to enhance lamb survival and carrying capacity in the wheat-sheep zone, without affecting grain yield (Newell & Hayes, 2017), especially if the forage were obtained by removal of surplus stubble after grain harvest, or prior to spike initiation in the next cycle. Early defoliation or grazing of winter wheat in southern Australia had limited impact on plant survival and grain yield (Newell et al., 2025), with reductions in shoot DM but not grain DM per unit of evapotranspiration (ET) at up to 22% of crop ET (Harrison et al., 2011). In contrast with reports implicating loss in plant stand for reduced grain yield in later regrowth cycles (Hayes et al., 2012; Larkin et al., 2014; Newell & Hayes, 2017), this study found that spike DM and grain DM pl^{-1} were reduced in the WS, following exposure to moderate water deficit in large soil columns in the previous DS (Figure 7). Further research is needed on the consequences of forage removal on subsequent performance of perennial wheat, and of DS water deficit on subsequent performance in the next WS.

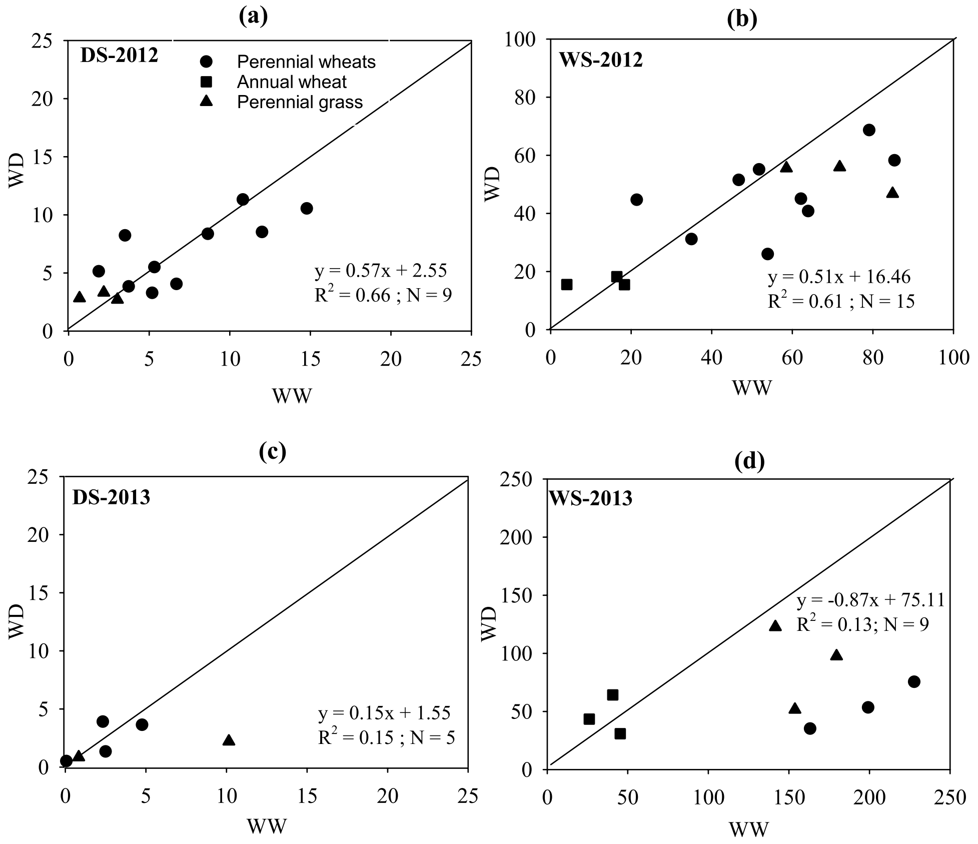

Figure 7. Above-ground DM (g pl^{-1}) for water-deficit (wd) and well-watered (WW) treatments in one annual wheat (square), four perennial wheats (circle) and one perennial grass (triangle): a) at the end of the 2012 DS; b) at maturity in the 2012 WS; c) at the end of the 2013 DS; and d) at maturity in the 2013 WS. In each case, DM in wd is plotted against DM in WW during the same season, relative to the 1:1 line. The linear regression between wd and WW is also shown for each season, together with its R^2, with * or n.S. ($p < 0.05$).

4.3. Allocation of dry matter

Among the perennial wheats, a higher proportion of shoot DM was allocated to stem in 235a, to grain in OK72, and to grain and roots in 11,955 (Figure 4). In contrast, the perennial grass 055 had a higher proportion allocated to crown and roots. While the perennial wheats did increase their investment of DM in structures associated with regeneration capacity (larger crown and roots relative to the annual), the perennial grass 055 invested a much higher proportion to crown and deep roots below 120 cm (Figure 5(d,f)). Our results were consistent with the preferential allocation of DM to regenerative traits (crown and deep roots) increasing with perenniality, and with the complete intermediate wheatgrass genome (6N; 055) having the strongest perenniality, as Larkin et al. (2014) also noted. It would be useful to better understand such responses in dry matter allocation, and to identify which traits contributed directly to improved adaptation.

In perennial wheat, active partitioning of DM to roots was demonstrated by its higher leaf-level photosynthetic capacity and stronger leaf-N related traits (e.g. chlorophyll, soluble protein, leaf N) than in annual wheat (Jaikumar et al., 2013). Nevertheless, source-sink manipulations also showed that perennial wheat was sink-limited, implying its DM was sufficient or in excess relative to its grain sink strength (Jaikumar et al., 2014). More recent studies in intermediate wheatgrass demonstrated slower establishment and preferential investment in roots (Fagnant et al., 2024), greater investment in perennial belowground structures after flowering (Fagnant et al., 2023), and lower mobilization of DM and N to spikes after flowering (Fagnant et al., 2025), relative to annual wheat. The combined evidence suggests strategic trade-off and higher overall productivity both contribute to higher DM allocation to roots over shoots in perennials, but further questions arise (see section 4.6).

4.4. Root growth and distribution

Root growth increased with plant age in successive WS (Figures 4(b,d,f) and 5(b,d,f)). Following reduced regrowth in the 2012 DS (Figures 4(c) and 5(c)), and presumably the

2013 DS (not recorded), there was a flush of shallow roots in the 2013 WS in all genotypes, and root DM increased from 30–90 cm in 11,955, and below 100 cm in perennial grass 055 (Figure 5(f)). Presumably, the increase in root DM at 0–30 cm was compensation for greater root loss in the 2013 DS, when plants were exposed to higher temperature and higher evaporative demand (Figure 1). This regrowth was essentially consistent with the findings of a study with intermediate wheat grass in Kansas, which found 25–40% of roots died off and grew back each year (Cox et al., 2006). Further, at intermediate depths (30–90 cm), root DM increased in 235a, 1195, OK72 and 055 in 2012 (Figure 5(d)), and especially in 11,955 in 2013 (Figure 5(f)). Below 100 cm, however, the largest increase in root DM was in 055 in both years, but especially in the 2013 WS. The data in Figure 5 show increases in root DM at depth in successive seasons, but it is not fully clear whether the extra roots came from the crown or from root branching, though some lateral roots were observed. Further investigation of root branching and turnover would also be warranted, especially to quantify the proportion of live roots, and those of lateral origin (e.g. Kano-Nakata et al., 2011).

4.5. Consequences of more roots at depth in perennials

Perennial wheats 235a, 11,955 and 055 had additional root DM at depth (Figure 5(d,f)), which was associated with additional tiller number in 11,955 and 055 (Figure 3(c)), and additional shoot DM in 235a, 11,955 and 055 (Figure 4(f)) in the 2013 WS. More roots at depth may be advantageous in coping with higher temperature and evaporative demand during the DS, presumably by facilitating some water uptake for transpirational cooling of shoots and crown to assist plant survival during the DS, and then to facilitate initial regrowth at the commencement of the following WS. This may also allow the plant to capture additional resources from deeper soil layers, for higher grain yield in subsequent years. These relationships between shoot growth, root growth and water extraction in the perennial wheats need to be examined further. A following paper will examine patterns of root growth and water extraction in four perennial wheats, a perennial grass and an annual wheat in a prolonged drying cycle, followed by rewatering.

4.6. Spike dry matter and grain dry matter per plant

While our results on spike DM and grain DM (Figure 6) were generally consistent with earlier reports in which yields of perennial grain crops were lower than those of their annual counterparts in the first two years (Jaikumar et al., 2012; Murphy et al., 2010), there is an upside here. Our results also demonstrate that perennial wheats could exceed annual wheat in total DM and especially in deep root DM (Figures 4 and 5). Further, perennial wheats could also produce spike DM equal to or even exceeding the annual wheat by the third year (Figure 6 (a-c)). This result implies that perennial wheats have the potential to equal or even exceed annual wheat in grain DM by the third year, once their initial priority to allocate additional DM to roots for survival and regeneration is established (Figure 5(b,d,f)).

In contrast, results from intermediate wheatgrass imply a long-term persistence strategy that favours investment in organs for regeneration rather than organs for reproduction (Fagnant et al., 2023, 2024, 2025). Nevertheless, a two-year study concluded that perennial wheat generally operated below its maximum photosynthetic capacity, so selection for greater sink strength should allow expression of higher photosynthetic capacity and higher grain yield (Jaikumar et al., 2013, 2014). This study adds to that, by suggesting that once investment in roots and reproductive structures is adequate in perennial wheat, more dry matter can then be directed to spikes and grain by the third year (Figures 4 and 6). Unfortunately, our grain DM data are not adequate to fully substantiate this, so further research is essential on DM allocation priority in perennial wheat, including field validation.

4.7. Harvest index and grain yield

At issue, however, is the proportion of shoot DM allocated to grain, which generally remains low (Table 1). Larkin et al. (2014) also reported that while shoot DM increased in perennial wheat over time, with a smaller increase in grain yield, HI would nevertheless continue to decline over time. Perennial wheats were later and taller and had more tillers (Figures 2 and 3), all of which could also contribute to their lower HI than annual wheat. Late maturity in the perennial grass 055 was associated with strong vernalization requirement (Innes et al., 2025), so its spike DM, grain DM and HI were reduced by exposure to higher temperatures. Perhaps timely grazing could assist by reducing any excess DM in the perennial wheats in later generations, without adversely affecting grain yield (Harrison et al., 2011; Newell et al., 2025), though this needs to be tested. Regardless, there is a need to select for higher HI in perennial wheat, as was achieved in annual crops in the Green Revolution (Evans, 1998). But the larger problem is the need for improved adaptation to Mediterranean field conditions. This may require backcrossing of perennial traits into adapted annual wheat genotypes, with selection for DS survival, WS regrowth, and improved spikelet fertility, especially under the higher temperatures and higher evaporative demand in Mediterranean environments, such as southern Australia.

4.8. Implications

Genomic complexity has been cited as a potential reason for the slower progress in improving perennial wheat (*T. aestivum* L. [6N]/*Th. intermedium* [6N] (Hayes et al., 2012; Larkin et al., 2014). In contrast, perennial rice only involves wide hybridization between *Oryza sativa* L. [2N] and *Oryza longistaminata* [2N], both with AA cytoplasm (Khush, 1997). Nevertheless, embryo rescue was still needed to obtain fertile progeny, and those combining high levels of spikelet fertility and longevity were rare (Zhang et al., 2022). Interestingly, from next-generation sequencing, only 16.16% of the genome of the released perennial rice cultivar PR23 was *O. longistaminata* (Zhang et al., 2022). As selection in perennial wheat proceeds, perhaps better-adapted amphiploids will be identified in future with only a small proportion of the genome from the perennial parent.

Perennial wheat 11,955 was able to nearly equal the perennial grass 055 in root DM, and to exceed the annual wheat Wedgetail and other perennial wheats in spike DM by the third year (Figures 4, 5, 6). In contrast to earlier reports, that a balanced genomic complement with complete chromosome sets from each parent could improve viability and perenniality (Larkin et al., 2014; Curwen-McAdams et al., 2016), 11,955 had only 40 chromosomes from *T. aestivum* and 16 from *Th. ponticum* (Morgan et al., 2023). This suggests more work is needed to better understand how chromosomes from perennial parents behave with the wheat genome, and what chromosome segments are needed for maintenance of both spikelet fertility and perennial regrowth over cycles.

Given the higher temperature and higher evaporative demand in the DS in Mediterranean environments such as southern Australia, improved traits for drought avoidance (deep roots for resource acquisition) and drought tolerance (dehydration tolerance and osmotic adjustment) may seem advantageous. While they may assist in delaying the inevitable, the DS stress is severe. We suggest that survival and performance of perennial wheat in these conditions would be more likely if the plants possessed summer dormancy, as advocated recently for perennial rice in similar conditions (Huang et al., 2025). At issue is the need to delay DS regrowth until after the rains recommence at the beginning of the next WS, as has been observed in some Australian perennial grasses (Norton et al., 2006; Volaire et al., 2014). Axillary bud dormancy would then allow the perennial crop to not attempt to use valuable resources, such as water and nutrients, when they are not yet available, or when their use may be wasteful, while conditions remain unfavourable for plant growth. Thus, a viable perennial grain need not retain green leaf cover all year; a better strategy when resources are seasonally scarce should be to delay new shoots, while retaining viable axillary buds and assimilate reserves for regrowth when seasonal conditions improve (Huang et al., 2025).

5. Conclusions

The results reveal how DM allocation priority differs between annual and perennial growth habit, with the perennials prioritising roots over shoots. The results then demonstrate that perennial wheats could exceed annual wheat in total and especially deep root DM. Further, perennial wheats could produce spike DM (Figure 6 (a-c)) equal to or even exceeding the annual wheat by the third year, once a suitable foundation for survival and regeneration was established. Contrary to previous reports, however, any reduction in performance in later cycles was associated with lower spike DM per plant, rather than in reduced plant stand. The results also suggested that deeper roots may be of benefit to access additional resources at depth during the dry season, to allow the plant to survive, and to regrow when water resources are replenished in the next wet season. This hypothesis is to be examined in the following paper.

Author contributions

CRediT: **Jesmin Akktar**: Data curation, Investigation, Formal analysis, Writing – original draft. **J. Sergio Moroni**: Methodology, Formal analysis, Supervision, Writing – original draft. **Mark R. Norton**: Methodology, Resources, Supervision, Writing – original draft. **Len J. Wade**: Conceptualisation, Funding acquisition, Formal analysis, Writing – Review and editing.

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Disclosure statement

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Abbreviations

DM	Dry matter
DS	Dry season
ET	Evapotranspiration
HI	Harvest index
MRD	Maximum root depth
WD	water-deficit
WS	Wet season
WW	Well-watered
055	CPI-148055
235a	CPI-147235a
280b	CPI-147280b
OK72	OK7211542

Data availability statement

The data associated with this manuscript are available from the authors on request.

References

Angus, J., Kirkegaard, J., & Peoples, M. (2001). Rotation, sequence and phase: Research on crop and pasture systems. In B. Rowe, D. Donaghy, & N. Mendham (Eds.), *Science and technology: Delivering results for agriculture? Proceedings 11th Australian Agronomy Conference* 29 January -1 February. Australian Society of Agronomy. www.agronomyaustraliaproceedings.org

Bell, L., Byrne, F., Ewing, M. A., & Wade, L. J. (2008). A preliminary whole-farm economic analysis of perennial wheat in an Australian dryland farming system. *Agricultural Systems*, *96* (1–3), 166–174.

Bell, L. W., Wade, L. J., & Ewing, M. A. (2010). Perennial wheat: A review of environmental and agronomic prospects for development in Australia. *Crop & Pasture Science*, *61*(9), 679–690. https://doi.org/10.1071/CP10064

Benjamin, J. G., & Nielsen, D. C. (2004). A method to separate plant roots from soil and analyse root surface area. *Plant and Soil*, *267* (1–2), 225–234. https://doi.org/10.1007/s11104-005-4887-3

Cassman, K. G., & Connor, D. J. (2022). Progress towards perennial grains for prairies and plains. *Outlook on Agric*. https://doi.org/10.1177/00307270211073153

Cattani, D. J. (2024). Perennial grains and oilseeds: Current status and future prospects. *Agriculture*, *14*(7), 1035. https://doi.org/10.3390/agriculture14071035

Chapman, E. A., Rubin, M. J., Tautges, N. E., Bowman, D. T., Crews, T. E., & DeHaan, L. R. (2022). Perennials as future grain crops: Opportunities and challenges. *Frontiers in Plant Science*, *13*, 898769. https://doi.org/10.3389/fpls.2022.898769

Cox, C. M., Murray, T. D., & Jones, S. S. (2002). Perennial wheat germplasm lines resistant to eyespot, *cephalosporium* stripe and wheat streak mosaic virus. *Plant Disease*, *86*, 1043–1048. https://doi.org/10.1094/PDIS.2002.86.9.1043

Cox, T., Glover, J. D., Van Tassel, D. L., Cox, C. M., & DeHaan, L. R. (2006). Prospects for developing perennial grain crops. *Bioscience*, *56*(8), 649–659. https://doi.org/10.1641/0006-3568(2006)56[649:PFDPGC]2.0.CO;2

Crews, T. E., Carton, W., & Olsson, L. (2018). Is the future of agriculture perennial? Imperatives and opportunities to reinvent agriculture by shifting from annual monocultures to perennial polycultures. *Global Sustainability*, *1*, e11. https://doi.org/10.1017/sus.2018.11

Cui, L., Ren, Y. K., Murray, T. D., Yan, W. Z., Guo, Q., Niu, Y. Q., Sun, Y., & Li, H. J. (2018). Development of perennial wheat through hybridization between wheat and wheatgrasses: A review. *Engineering*, *4*(4), 507–513. https://doi.org/10.1016/j.eng.2018.07.003

Curwen McAdams, C., Arterburn, M., Murphy, K. M., Cai, X. W., & Jones, S. S. (2016). Towards a taxonomic definition of perennial wheat: A new species *xTritipyrum aaseae* described. *Genetic Resources and Crop Evolution*, *2016*. https://doi.org/10.1007/s10722-016-0463-3

Curwen McAdams, C., & Jones, S. S. (2017). Breeding perennial grain crops based on wheat. *Crop Science*, *57*(3), 1172–1188. https://doi.org/10.2135/cropsci2016.10.0869

Evans, L. T. (1998). *Feeding the ten billion: Plants and population growth*. Cambridge University Press.

Ewel, J. J., Schreeg, L. A., & Sinclair, T. R. (2018). Resources for crop production: Accessing the unavailable. *Trends in Plant Science*. https://doi.org/10.1016/j.tplants.2018.10.008

Fagnant, L., Aubry, P., Duchene, O., Jungers, J. M., & Dumont, B. (2025). Seasonal allocation of dry matter and nitrogen in *th. intermedium* across stand ages. *The European Journal of Agronomy*, *164*, 127522. https://doi.org/10.1016/j.eja.2025.127522

Fagnant, L., Delaplace, P., Delory, B. M., & Dumont, B. (2024). *Thinopyrum intermedium* showed a slower establishment phase compared to winter wheat in a controlled environment. *Agrosystems, Geosciences & Environment*, *8*, e70021. https://doi.org/10.1002/agg2.70021

Fagnant, L., Duchene, O., Celette, F., David, C., Bindelle, J., & Dumont, B. (2023). Learning about the growing habits and reproductive strategy of *thinopyrum intermedium* through the establishment of its critical nitrogen dilution curve. *Field Crops Research*, *291*, 108802. https://doi.org/10.1016/j.fcr.2022.108802

Galassi, E., Natale, C., Nocente, F., Taddei, F., Visioli, G., Ceccarelli, S., Galaverna, G., & Gazza, L. (2025). Regenerative agronomic approaches: Technological, biochemical and rheological characterization of four perennial wheat lines grown in Italy. *Agronomy*, 15. https://doi.org/10.3390/agronomy15040939

Glover, J. D., Reganold, J. P., Bell, L. W., Borevitz, J., Brummer, E. C., Buckler, E. S., Cox, C. M., Cox, T. S., Crews, T. E., Culman, S. W., Dehaan, L. R., Eriksson, D., Gill, B. S., Holland, J., Hu, F., Hulke, B. S., Ibrahim, A. M. H., Jackson, W., Jones, S. S., . . . Xu, Y. (2010). Increasing food and ecosystem security via perennial grains. *Science*, *328*(5986), 1638–1639. https://doi.org/10.1126/science.1188761

Harrison, M. T., Evans, J. R., Dove, H., & Moore, A. D. (2011). Recovery dynamics of rainfed winter wheat after livestock grazing, 1. Growth rates, grain yields, soil water use and water-use efficiency. *Crop & Pasture Science*, *62*(11), 947–959. https://doi.org/10.1071/CP11234

Hayes, R. C., Newell, M. T., DeHaan, L. R., Murphy, K. M., Crane, S., Norton, M. R., Wade, L. J., Newberry, M., Fahim, M., Jones, S. S., Cox, T. S., & Larkin, P. J. (2012). Perennial cereal crops: An initial evaluation of wheat derivatives. *Field Crops Research*, *133*, 68–89. https://doi.org/10.1016/j.fcr.2012.03.014

Hayes, R., Wang, S., Newell, M., Turner, K., Larsen, J., Gazza, L., Anderson, J., Bell, L., Cattani, D., Frels, K., Galassi, E., Morgounov, A., Revell, C., Thapa, D., Sacks, E., Sameri, M., Wade, L. J., Westerbergh, A., Shamanin, V., . . . Li, G. (2018). The performance of early-generation perennial winter cereals at 21 sites across four continents. *Sustainability*, *10*(4), 1124. https://doi.org/10.3390/su10041124

Huang, G. F., He, M., Wang, S. L., Li, Y. F., Li, J. L., Zhang, Y. J., Zhang, S. L., Lian, X. P., Zhang, J., Wade, L. J., & Hu, F. Y. (2025). Perennial rice regrowth responds to stubble characteristics, temperature and genotype. *Field Crops Research*, *322*, 109746. https://doi.org/10.1016/j.fcr.2025.109746

Huang, G. F., Qin, S. W., Zhang, S. L., Cai, X. L., Wu, S. K., Dao, J. R., Zhang, J., Huang, L. Y., Harnpichitvitaya, D., Wade, L. J., & Hu, F. Y. (2018). Performance, economics and potential impact of perennial rice PR23 relative to annual rice cultivars at multiple locations in Yunnan Province of China. *Sustainability*, *10*(4), 1086. https://doi.org/10.3390/su10041086

Innes, P. J., Newell, M. T., Pembleton, K. G., Hayes, R. C., & Radanielson, A. N. (2025). A study of the vernalization requirement of mountain rye (Secale strictum syn. S. montanum) may help explain low grain yields of perennial cereals compared to wheat. *AoB Plants*, *2025*, 17plaf015. https://doi.org/10.1093/aobpla/plaf015

Jaikumar, N. S., Snapp, S. S., Flore, J. A., & Weiser, R. L. (2013). Life history and resource acquisition: Photosynthetic traits in selected accessions of three perennial cereal species compared with annual wheat and rye. *American Journal of Botany*, *100*, 2468–2477. https://doi.org/10.3732/ajb.1300122

Jaikumar, N. S., Snapp, S. S., Flore, J. A., & Weiser, R. L. (2014). Photosynthetic responses in annual rye, perennial wheat, and perennial rye subjected to modest source: Sink ratio changes. *Crop Science*, *54*, 274–283. https://doi.org/10.2135/cropsci2013.04.0280

Jaikumar, N. S., Snapp, S. S., Murphy, K., & Jones, S. S. (2012). Agronomic assessment of perennial wheat and perennial rye as cereal crops. *Agronomy Journal*, *104*(6), 1716–1726. https://doi.org/10.2134/agronj2012.0291

Kano-Nakata, M., Inukai, Y., Wade, L. J., Siopongco, J., & Yamauchi, A. (2011). Root development, water uptake, and shoot dry matter production under water deficit conditions in 2 CSSLs of rice: Functional roles of root plasticity. *Plant Production Science*, *14*(4), 307–317. https://doi.org/10.1626/pps.14.307

Khush, G. S. (1997). Origin, dispersal, cultivation and variation in rice. *Plant Molecular Biology*, *35*(1–2), 25–34. https://doi.org/10.1023/A:1005810616885

Larkin, P. J., Newell, M. T., Hayes, R. C., Aktar, J., Norton, M. R., Moroni, J. S., & Wade, L. J. (2014). Progress in developing perennial wheats for grain and grazing. *Crop & Pasture Science*, *65*(11), 1147–1164. https://doi.org/10.1071/CP13330

Loomis, R. S. (2022). Perils of production with perennial polycultures. *Outlook on Agriculture*. https://doi.org/10.1177/00307270211063910

Morgan, R., Danilova, T., Newell, M., Cai, X., & Jones, S. S. (2023). Agronomic evaluation and molecular cytogenetic characterization of Triticum aestivum × Thinopyrum spp. derivative breeding lines presenting perennial growth habits. *Plants*, *12*(18), 3217. https://doi.org/10.3390/plants12183217

Morgounov, A., Shchuklina, O., Pototskaya, I., Aydarov, A., & Shamanin, V. (2025). Perennial grains in Russia: History, status, and perspectives. *Crops*, *5*, 46. https://doi.org/10.3390/crops5040046

Murphy, K. M., Lyon, S. R., Balow, K. A., & Jones, S. S. (2010). Post-sexual cycle regrowth and grain yield in *thinopyrum elongatum* × *triticum aestivum* amphiploids. *Plant Breeding*, *129*(5), 480–483. https://doi.org/10.1111/j.1439-0523.2009.01712.x

Newell, M. T., & Hayes, R. C. (2017). An initial investigation of forage production and feed quality of perennial wheat derivatives. *Crop & Pasture Science*, *68*(12), 1141–1148. https://doi.org/10.1071/CP16405

Newell, M. T., Hayes, R. C., Refshange, G., Holmes, B. W. B., Munday, N., Hopkins, D. L., & Li, G. (2025). Choice of companion legume influences lamb liveweight output and grain yield in a dual-use perennial wheat/legume intercrop system. *Animal Production Science*, *65*, AN24246. https://doi.org/10.1071/AN24246

Norton, M. R., Lelievre, F., & Volaire, F. (2006). Summer dormancy in *Dactylis glomerata* L.: The influence of season of sowing, and a simulated mid-summer storm on two contrasting cultivars. *Australian Journal of Agricultural Research*, *57*(5), 565–575. https://doi.org/10.1071/AR05237

Samson, B. K., Voradeth, S., Zhang, S. L., Tao, D., Xayavong, S., Khammone, T., Douangboupha, K., Sihathep, V., Sengxua, P., Phimphachanhvongsod, V., Bouahom, B., Jackson, T. A., Harnpichitvitaya, D., Hu, F. Y., & Wade, L. J. (2018). Performance and survival of perennial rice derivatives (*Oryza sativa* L./*Oryza longistaminata*) in Lao PDR. *Experimental Agriculture*, *54*, 592–603. https://doi.org/10.1017/S0014479717000266

Steel, R. G. D., & Torrie, J. H. (1960). *Principles and procedures of statistics*. McGraw-Hill Book Company.

Tilman, D., Balzer, C., Hill, J., & Befort, B. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Science USA*, *108*(50), 20260–20264. https://doi.org/10.1073/pnas.1116437108

Tsitsin, N. V., & Lyubimova, V. F. (1959). New species and forms of cereals derived from hybridization between wheat and couch grass. *The American Naturalist*, *93*, 181–191. https://doi.org/10.1086/282073

Turner, N. C. (2004). Agronomic options for improving rainfall-use efficiency of crops in dryland farming systems. *Journal of Experimental Botany*, *55*(407), 2413–2425. https://doi.org/10.1093/jxb/erh154

Volaire, F., Barkaoui, K., & Norton, M. R. (2014). Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions. *European Journal of Agronomy*, *52*(B), 81–89. https://doi.org/10.1016/j.eja.2013.10.002

Wagoner, P., & Schaeffer, J.R. (1990). Perennial grain development: Past efforts and potential for the future. *Critical Reviews in Plant Sciences*, *9*, 381–408. https://doi.org/10.1080/07352689009382298

Zadoks, J. C., Chang, T. T., & Konzac, C. F. (1974). A decimal scale for the growth stages of cereals. *Weed Research*, *14*, 415–421. https://doi.org/10.1111/j.1365-3180.1974.tb01084.x

Zhang, S. L., Hu, J. A., Yang, C. D., Haitao, L., Yang, F., Zhou, J. H., Samson, B. K., Boualaphanh, C., Huang, L. Y., Huang, G. F., Zhang, J., Huang, W. Q., Tao, D., Harnpichitvitaya, D., Wade, L. J., & Hu, F. Y. (2017). Genotype by environment interactions for grain yield of perennial rice derivatives (*Oryza sativa* L./*Oryza longistaminata*) in southern China and Laos. *Field Crops Research*, *207*, 62–70. https://doi.org/10.1016/j.fcr.2017.03.007

Zhang, S. L., Huang, G. F., Zhang, J., Huang, L. Y., Cheng, M., Wang, Z. L., Zhang, Y. N., Wang, C. L., Zhu, P. F., Yu, X. L., Tao, K., Hu, J. A., Yang, F., Qi, H. W., Li, X. P., Liu, S. L., Yang, R. J., Long, Y. C.,Harnpichitvitaya, D., . . . Hu, F. Y. (2019). Genotype by environment interactions for performance of perennial rice genotypes (*Oryza sativa* L./*Oryza longistaminata*) relative to annual rice genotypes over regrowth cycles and locations in southern China. *Field Crops Research*, *241*, 107556. https://doi.org/10.1016/j.fcr.2019.107556

Zhang, S. L., Huang, G. F., Zhang, Y. J., Lv, X. T., Wan, K. J., Liang, J., Feng, Y. P., Dao, J. R., Wu, S. K., Zhang, L., Yang, X., Lian, X. P., Huang, L. Y., Shao, L., Zhang, J., Qin, S. W., Tao, D. Y., Crews, T. E.Sacks, E., J., . . . Hu, F. Y. (2022). Sustained productivity and agronomic potential of perennial rice. *Nature Sustainability*, *6*, 28–38. https://doi.org/10.1038/s41893-022-00997-3